Survey of ephemeral pool invertebrates at Wupatki NM: an evaluation of the significance of constructed impoundments as habitat.

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ABSTRACT

Ephemeral aquatic habitats in Wupatki National Monument vary from naturally formed pools in arroyos over 5000 years old, to constructed catchment basins with ages estimated at 60-1000+ years old, and borrow pits and stock ponds 30-60 years old. The different ages of these pools provide different histories of colonization by amphibians and aquatic invertebrates, especially temporary pool specialists such as spadefoot toads and branchiopod crustaceans. Ten pools of five different origins and ages were surveyed in August and/or September 1997 for aquatic organisms; a total of 13 surveys were conducted. A total of 22 taxa were found, the number of species in a given pool during a given survey ranged from 1 to 10. Species composition of the communities changed from one sampling date to the next within individual pools. There appears to be some relationship between age of the pool and community structure, but it is not direct: species richness was not directly correlated with pool age. Other factors such as pool size (= longevity) and distance from source populations may also be important in structuring ephemeral pool communities.

INTRODUCTION

Ephemeral pools can be found in many parts of the world. These pools range in size from small rock basins holding no more than a litre or two, to large playa lakes covering hundreds of hectares. They occur at high elevations, below sea level, on bedrock, on very old soils and recent volcanic surfaces. They fill in different seasons depending on climatic patterns, and may have a single annual wet phase, or fill and dry many times a year. Ephemeral pools form through natural geomorphic processes or they may result from human activity (e.g., constructed catch basins, inadvertent damming by roadbeds, etc.) Many pools are heterotrophic, much of the energy passing through them comes from detritus, not direct photosynthetic production (Kuller and Gasith 1996). Pools supporting a wetland/terrestrial plant community (e.g., vernal pools in California's Central Valley) may be autochthonous in that vascular plant production during the dry phase provides detritus that supports the aquatic system during the next wet phase. Some systems (e.g., rock pools and playas) lack significant vascular plant production, much of their energy may come from allochthonous detritus blown in or carried into the basin from the surrounding watershed, with primary production by algae in the basin varying in significance.

Little is known in general about what determines species composition of ephemeral pool invertebrate communities. Ephemeral pools typically have a fairly simple community structure, but species composition can vary significantly (Thiery 1991, Jeffries 1994, Anderson et al. 1999)). Most pools are populated with widespread species, but some species are endemic to particular geographic regions, or pool conditions. Much of the diversity in ephemeral pools may still be undocumented, as evidenced by a recent survey of California Central Valley pools, where as many as 52% of the crustaceans encountered were reported from California for the first time, and up to 44% may be new species (King et al. 1996).

Ecologists hope to find patterns among communitites that indicate a few physical and biological parameters determine community structure. While there appear to be some commonality in the structure of macroinvertebrate communities found in ephemeral pools, it is not clear whether ephemeral pool community structure is predictable. Pool inhabitants are either aquatic opportunists, species that occupy both temporary and permanent waters, or specialists with precise adaptations for living in temporary aquatic environments (Wiggins et al. 1980, Williams 1985). Typically there is at least one large branchiopod crustacean, often a fairy shrimp, if only a single branchiopod is present. Branchiopods are one of the quintessential ephemeral pool groups, limited almost entirely to temporary bodies of water. The presence of more than one branchiopod, in particular, more than one anostracan, in a single pool has been characterized as rare by many authors(Dexter and Kuehnle 1951, Dexter 1953, Moore 1970, Anderson 1974, Maynard and Romney 1975, Donald 1982). Other studies indicate the occurrence of three or more branchiopod species in a single pool community is fairly common, although there may be only a single fairy shrimp species present (Horne 1967, 1974, DeBrey et al. 1991, Thiery 1991, Graham 1995). (Maeda-Martinez et al. 1997) report up to eight species in three orders in a single pool in northern Mexico. Aquatic insects are represented by many orders, the species present depend on pool longevity, nearness to permanent water, and abundance of other invertebrates as predators or prey. Groups usually found are beetles (e.g., Dytiscidae and Hydrophilidae), backswimmers, water boatmen, and a variety of fly larvae (e.g., Chironomidae, Ceratopogonidae, Culicidae).

Arizona has a very diverse branchiopod fauna, with more fairy shrimp species than any other state except California (Belk 1977, Eng et al. 1990, Eriksen and Belk 1999, Belk and Fugate 2000). The topographic diversity of the state, along with climatic and chemical (especially salinity) gradients are largely responsible for this diversity (Belk 1977). (Sellers and Hill 1974) divided Arizona into six climatic physiographic sections, and (Belk 1977) found that fairy shrimp distributions correlated well with these sections. Wupatki lies near the boundaries of Plateau and Northeast sections, and thus there is a potential for a relatively diverse fairy shrimp fauna, and prossibly other branchiopods as well. Two species of *Triops* may be found in Arizona; *T. longicaudatus* has been recorded in northern Arizona, and (Sassaman et al. 1997) identified a second species, *T. newberryi*, from specimens collected in southern Arizona.

Essentially nothing is known about the invertebrate communities in ephemeral pools of Wupatki NM. Tadpole shrimp were collected from a single location within Wupatki (Cinnamon 1989); it is not known if any were collected or what species they were. No systematic surveys have been made of ephemeral pools at Wupatki National Monuments to determine presence of branchiopods, or of other aquatic invertebrates.

Distance from permanent water to an ephemeral pool will affect which species can colonize that pool, and thus structure of the invertebrate/amphibain community will be driven by this distance to some extent. Species capable of dispersing greater distances will probably occur in more pools overall, and are more likely to occur in isolated pools than are species of lower vagility. Species with poor dispersal abilities are predicted to be more common in pools nearer more permanent water. Most branchiopod crustaceans are found only in ephemeral pools. On the Colorado Plateau, branchiopods probably disperse primarily as cysts carried by wind. Cysts are predicted to be found in any pool that has been on the landscape long enough that cysts have had a chance to blow into them. Active branchiopod populations will be found in pools that meet the life history requirements of the particular species (Williams 1987).

On a natural landscape, ephemeral pools in an area are usually of approximately the same age, and thus potential colonization is probably equivalent and community structure of similar pools is probably driven by pool size and spatial arrangement of pools. In human-altered landscapes, pools of different ages may be in close proximity, providing different opportunities for colonization over time. Older pools will have had a longer time for species to colonize them, thus low vagility species (e.g., amphibians) and passive dispersers (e.g., branchiopods) are predicted to be found in older pools more often than younger pools. The invertebrate communities of a catch basins might be influenced not only by age of basin, but also proximity to permanent water and/or older pools; a young catchment near an old pool should be more similar to the nearby older pools than if the impoundment was more isolated.

There is a gradient in distance to permanent water among the pools surveyed at Wupatki NM as well as a temporal gradient in ages of the pools. Community structure in these pools is probably influenced by dispersal ability of the different organisms. Older pools will have had a longer time for species to colonize, thus species with low vagility are predicted to be found in older pools but less likely in younger pools. Species with poor dispersal ability are also predicted to be more common in pools that are near more permanent water bodies. Passive dispersers such as branchiopods would be expected to be found in older pools, and possibly pools near old (usually natural) pools. Organisms that do not disperse readily (e.g., very aquatic insects, amphibians, etc.) are more likely to be limited to pools nearer permanent water than strong fliers such as backswimmers and some beetles.

Geologic conditions at WUPA are not conducive to the formation of natural ephemeral pools. There are few exposures of rock strata that develop weathering pits, and geomorphic processes have developed typical dendritic drainage patterns rather than closed basins. There were only two kinds of natural ephemeral pools encountered in surveys at WUPA, both in drainages: 1) Small rock pools eroded as washes cut through thin sandstone layers of the Moenkopi Formation. 2) Cinder and mud flows have blocked larger washes such as Deadman Wash and Kanà'à Wash, forming long, relatively shallow pools behind these dams. (Cinnamon 1989) collected tadpole shrimp from at least one such pool in Deadman's Wash (Wupatki). However, the dams are so numerous, there is very little effective watershed for any of the segments. Precipitation must be quite heavy directly over one of these segments, or a side cañon for it to fill. Given the spatial unpredictability of summer thunderstorms, the filling of any given pool is very unpredictable. The only two containing water during either survey were both adjacent to, and downstream from the entrance road. They probably fill more frequently now than other segments of Deadman Wash because their watersheds include a large stretch of road.

Wupatki National Monument presents an unusual opportunity to explore the ecology of ephemeral pool invertebrate communities and examine the role of dispersal in structuring these communities. There are no permanent surface water sources within Wupatki, and most relatively permanent water near the monument has been developed from wells in the last 150 years (N. Tancredo, Wupatki NM, pers. comm.). The Little Colorado River, and a series of small springs are the only natural water sources in the area, and even the Little Colorado River does not always have surface water near Wupatki NM. Aquatic insects will disperse from these permanent water refugia to ephemeral pools following rains, distance will filter insect species with different dispersal abilities. Because many of the insects colonizing ephemeral pools are predators, the species composition of a pool may be determined in part by what other species are present.

Native Americans constructed numerous check dams and other catchments within Wupatki's boundaries (Baldwin and Bremer 1986, Anderson 1990) that have been colonized over time by ephemeral pools species. Branchiopods can be very numerous in a pool; up to 20,000 fairy shrimp have been estimated in pools containing only about 200 l of water (T. B. Graham, unpublished data). It is not known if these crustaceans were used as food by the Sinagua or Navajo, but there is evidence that branchiopods have been and still are used by some cultures for food (Sanoamuang and Dumont 2000), D. Belk, pers. comm.). Branchiopods represent an additional, readily available, source of protein and energy (Driver 1981). Construction of water catchments was most likely to collect and store limited precipitation, but these impoundments increased available habitat for branchiopods, thus increasing their abundance and perhaps availability as a food item.

A number of predictions can be made about how ephemeral pool communities might be structured. Results of Wupatki surveys may provide support for some or all of these predictions, evn though the Wupatki study was not designed to explicityl test these theories. Predictions are:

1. Older pools are more likely to have slow dispersing species (e.g., amphibians), and passive dispersers (e.g., branchiopod crustaceans).
2. Isolated young pools will have simpler communities (fewer species) than young pools nearer to permanent water.
3. Frequently disturbed pools (e.g., flow-through pools in washes) will have simpler communities. Disturbance can override other factors influencing community structure.
4. Older pools will have higher species richness than young pools, other factors being equal.
5. "More aquatic" species will be more common in pools near permanent water than in pools distant from other water sources.
6. Ephemeral pool communities will be more diverse in larger pools (typically last longer).
7. Ephemeral pool communities will be more diverse following large rains, or multiple rain events (more opportunities for dispersal).
8. Larger cysts disperse more slowly than smaller cysts; higher wind velocities, which are less frequent, are needed to carry larger cysts, thus species with large cysts should be limited to older pools.

The objectives of this research are to: 1) survey Wupatki NM to locate ephemeral pools and classify them as natural or constructed; 2) measure pool physical and chemical parameters; 3) sample and identify aquatic invertebrates in all pools with water; and 4) correlate invertebrate community composition with pool size, distance to permanent water, and pool type (natural or constructed); work with interpretive staffs of all three parks to develop interpretive materials describing the natural history of ephemeral pool ecosystems, and the possible cultural significance of these organisms.

METHODS

Study Site

Wupatki National Monument is located in north-central Arizona, about 50 km (30 miles) from Flagstaff (Figure 1). The monument encompasses mostly Permian Kaibab Limestone and Triassic Moenkopi Formation, with some lava and cinder deposits (Chronic 1986). Elevation of Wupatki NM ranges from 1370 to 1680 m (4500 to 5500 ft) above sea level (N. Tancredo, unpubl. GIS data from Wupatiki NM) .

Survey methods

Six ephemeral pools were surveyed on 16-17 August 1997 and seven pools were surveyed 17 September 1997. Three of these pools were surveyed in both August and September. All pools encountered with water on these dates were surveyed. Maximum size was estimated for each pool by measuring widths, lengths and depths. Pools were classified as roughly circular, rectangular or triangular, and surface areas calculated with appropriate formulae. Volumes were estimated as half an ellipsoid: $\{(2/3)*o*(L/2)*(W/2)*(D)\}$ where L = maximum pool length, W = maximum pool width perpendicular to length and D = maximum pool depth (Haefner and Lindahl 1991, Anderson et al. 1999). Current pool surface area and volume were also estimated for each pool in the same way. Pool locations were geo-referenced with a GPS; elevation and distances to permanent water sources were determined with a GIS. The age of each pool was assigned based on archeological and historical records. The natural rock pools were given an arbitrary age of 5,000 years to distinguish them from the newer pools. Cinder cones formed from eruptions beginning about 1064 A.D. and continuing for at least 100 years (Chronic 1986), thus pools formed from cinder dams in Deadman Wash were assigned an age of 700 years. Arrowhead Tank was constructed about 1960 (J. DeYoung, pers. comm.), but it is in a natural cloased basin--a karst feature resulting from dissolution of Kaibab Limestone. Initial analyses used 40 years for the age of Arrowhead Tank, but data were also analyzed with an age of 1000 years as an estimated age for the closed basin.

Each pool was exhaustively surveyed for macroinvertebrates and amphibians by sweeping with an aquatic net. In most pools, the entire pool was swept more than once; in large pools, approximately 20-50% of the pool surface area was swept. All organisms caught in the net were placed in a shallow pan of water. Sweeps continued until three consecutive sweeps added no new species. Voucher specimens were collected and placed in 70% isopropyl alcohol, all other organisms were returned to the pools. Neither absolute nor relative abundances were estimated for organisms in pools, species were scored as present or absent from a pool during a given survey. The branchiopods were identified to species using (Belk 1975, Belk 1989, Maeda-Martinez et al. 2000). Insects were identified to genus (except the Chironomidae) using (Thorp and Covich 1991, Merrit and Cummins 1996); chironomids were identified only to family. Tadpoles all had at least hind feet, thus they could be separated into either *Spea* or *Bufo* in the field. Toadlets were identified using (Stebbins 1985), and tadpoles of the same genus were assumed to be of the same species.

Community structure was compared among pools and sample dates using NMS and cluster analysis (McCune and Mefford 1999, McGarigal et al. 2000). The Sorensen's similarity index: $S = 2C/(A + B)$ (Southwood and Henderson 2000) was used to compare communities in pools surveyed in both August and September. Analyses were made using species presence/absence data, coupled with a matrix of environmental factors listed in Table 1.

RESULTS AND DISCUSSION

A total of 22 taxa were found at least once in the 13 surveys of 10 pools at Wupatki NM (Table 2). Five species of branchiopods were found, three species of fairy shrimp, a single species of tadpole shrimp and a single clam shrimp species (Table 2). Two amphibian species, five genera in two families of Coleoptera (beetles), and two genera each of Notonectidae, Corixidae and Culicidae were found.

Eleven species were found in both August and September (Table 2). Five species were found only in August; three of these occurred in only one pool. The other two species were relatively common; the spadefoot *Spea multiplicatus* was found in five of the six pools surveyed, the beetle *Hydrochus* sp. occurred in three of six pools (Table 2). Six species were found only in September. Four taxa occurred in one pool each, the other two species were found in either two pools or three pools (Table 2).

The mosquito *Psorophora* sp. was found in six pools, more than any other species. *Psorophora* sp. occurred in three pools in August, two small natural rock pools (NN1a and NN3a, see Table 2 for pool names and abbreviations) and one small impoundment (NI1a), all in close proximity to each other. In September, *Psorophora* sp. was found in the two large pools in Deadman Wash (DM1s and DM2s) and the very large stock tank, ATs. Psorophora mosquitoes lay eggs that tolerate dessication, and it is the egg stage that carrys the population from one rain to the next (Bohart and Washino 1978). They are among the first colonizers of an ephemeral pool, since the eggs are already present, and only have to hatch (Bohart and Washino 1978).

Tadpoles of the New Mexico spadefoot, *Spea multiplicatus*, were found in five of the six pools surveyed in August (Table 2). It was absent only from the smallest of the three natural rock pools (NN1a) in a small wash. Since tadpoles were found in the two larger pools (NN2a and NN3a) just below this little pool (within 5-10 m), it is likely the pool was too small for female spadefoots to choose to lay eggs in it. Tadpoles also occurred in DM1a, CWa and NI1a. No spadefoot tadpoles, metamorphs, or adults were found in any of the September surveys.

The fairy shrimp *Streptocephalus dorothae* was one of two species that occurred in four pools, and was found in both August and September surveys. In August it was found in CWa and NI1a; ATs, DM2s, and CWs all contained *S. dorothae* in September. All these pools except DM2s are man-made impoundments (although AT was constructed in a natural closed basin), and even DM2 receives much of its water from the road. (Maynard and Romney 1975) report *S. dorothae* is primarily found in short grass steppe close to the foothills of the Rocky Mountains, in prairie swale pools. They refer to a population of *S. dorothae* in a sandstone pothole as "possibly unique for the species." (Maynard and Romney 1975, p. 10). At Wupatki NM, *S. dorothae* was found in both natural and man-made pools (Table 2), but all of them resembled prairie swale pools. While Mackin (1942) states *S. dorothae* prefers clear water with vegetation, none of the Wupatki NM pools fit this description--visibility in four of the five pools with *S. dorothae* was less than 1 cm. In surveys of over 200 natural rock pools and stock tanks in southern Utah, I have found *S. dorothae* only in man-made basins (T. B. Graham, unpubl. data). *Streptocephalus dorothae* may be dispersed by lighter winds (smaller and/or lighter cysts), and thus reaches pools before other species of fairy shrimp, or perhaps it has broader tolerance levels for water chemistry, since earth dam catchments probably have higher solute concentrations than potholes in sandstone.

The other species that occurred in four pools, the water boatman *Callicorixa* sp., also was found in both August and September surveys. In August, *Callicorixa* sp. occurred in CWa and NI1a, it was found only in the two borrow pits (WBs and SBs) in September. The backswimmer, *Notonecta* sp., occurred in four surveys, but only three pools. It occurred in the two impoundments, CWa and NI1a, in August, and in DM2s and CWs in September.

The tadpole shrimps found at Wupatki NM were quite different from those of southeastern Utah. Their bodies were much shorter, although the number of body segments still seems within the range for both *Triops longicaudatus* and *T. newberryi (Sassaman et al. 1997)*. (Maeda-Martinez et al. 2000) propose a third species, *T. oryzaphaga*, differing morphologically from the other two species in the total number of body rings, and number of limbless abdominal segments. Material from Wupatki NM was tentatively identified as *T. newberryi* based on the total number of body rings, and the number of legless rings as established by (Maeda-Martinez et al. 2000).

Triops newberryi, Branchinecta lindahli and *Eulimnadia cylindrova* were surprisingly rare. *Triops newberryi* occurred only in DM1a and DM2s, and ATs, which were the oldest pools, and largest except for the borrow pits. *Eulimnadia cylindrova* was found only in NI1a in August, and *B. lindahli* was found only in September in WB. Dispersal to new habitats by branchiopods is a passive process (Wiggins et al. 1980, Williams 1985, Williams 1987); on the Colorado Plateau, the primary dispersal mechanism is probably wind. Cyst size could influence dispersal; higher wind speeds are required to move larger particles . *Thamnocephalus platyurus* was also limited to the large, older pools (Table 2). Egg sizes of a number of branchiopods are given in Table 3, taken from (Belk 1989, Brendonck et al. 1993). *Triops newberryi, E. cylindrova, B. lindahli* and *T. platyurus* all have larger cysts than *S. dorothae* (Table 3), which could explain the relative rarity of these four species at Wupatki NM. It is somewhat surprising that *B. lindahli* had such a limited distribution, since it is quite common across western North America, being given the name of "versatile fairy shrimp" by (Eriksen and Belk 1999). (Hill and Shepard 1997) measured 89 *B. lindahli* cysts, and found cysts that were as small as S. dorothae, and as large as T. platyurus ((Hill and Shepard 1997), Figure 1). Long distance dispersal by *B. lindahli* may be achieved by smaller cysts, larger cysts would be more likely to remain in pools where they were generated. *Branchinecta lindahli* and *Streptocephalus dorothae* are the two species most often found in man-made ephemeral pools in southern Utah (T. B. Graham, pers. obser.), indicating that *B. lindahli* is capable of widespread dispersal. It is not clear why this species occurred in only one survey at Wupatki NM.

The proportion of surveys in which a species was found is an indication of how widespread species are, and of similarities that may be found among communities. Figure 2a shows the distribution of species in surveys; over half the species (54.5%) were found in less than 15% of the surveys (one or two surveys). Some of the species found in more than one survey (e.g., *Gerris* sp.) were actually only seen in one pool. Ten species occurred in only one of the ten ephemeral pools surveyed. Figure 2b presents the proportion of surveyed pools in which each species was observed; this emphasizes the lack of similarity between communities in Wupatki NM ephemeral pools.

Nine of the 12 species occurring in only one or two surveys are insects that can fly from more permananet water sources. Two of these species, *Culex* sp. and *Callibaetis* sp., were fairly numerous in these pools, but other species were represented in net sweeps by only one or a few individuals. Individuals dispersing from permanent water probably move in all directions, few individuals may actually arrive at the same pool. The single specimen of *Hydrophilus* sp. was found trying to burrow under an algal mat in about 1 cm of water in the Wukoki borrow pit (WB). This individual likely probably dispersed shortly after recent rains, and selected WB when there was more water in it. WB has a large surface area (Table 1), which may be used as a cue to select new habitats. Volume of water in WB was actually quite small, and evaporation quickly removed most of the water.

The majority of species observed in the August and September surveys were rare, 12 of 22 species occurred in only one or two surveys (Figure 2a). The mosquito, *Psorophora* sp., was found in six surveys, three of six pools in August, and three different pools of the seven pools surveyed in September. When pool surveys of the same pool in August and September are combined, the rarity of most species is even more apparent. Figure 2b shows that ten of 22 species were found in only one pool. Nine of the 12 species occurring in only one or two surveys are insects that can fly from more permananet water sources. Two of these species, *Culex* sp. and *Callibaetis* sp., were fairly numerous in these pools, but many were represented in net sweeps by only one or a few individuals. Individuals dispersing from permanent water probably move in all directions, few individuals may actually arrive at the same pool. The single specimen of *Hydrophilus* sp. was found trying to burrow under an algal mat in about 1 cm of water in the Wukoki borrow pit (WB). This individual likely probably dispersed shortly after recent rains, and selected WB when there was more water in it. WB has a large surface area (Table 1), which may be used as a cue to select new habitats. Volume of water in WB was actually quite small, and evaporation quickly removed most of the water.

Three species with relatively poor dispersal abilities occurred in single pools: *Branchinecta lindahli*, *Eulimnadia cylindrova*, and *Bufo punctatus*. The two branchiopods, *B. lindahli* and *E. cylindrova*, were each found in one man-made pool. Both pools were long distances from permanent water, and while not very far from natural pools, the branchiopods were found only in these individual pools; the nearest pools with populations of these species is unknown. Branchiopod dispersal on the Colorado Plateau is thought to be primarily via wind; establishment of a population in any particular pool is probably a stochastic event.

The red-spotted toad, *Bufo punctatus*, was present in both surveys of Coyote Water, but found in no other pools. Coyote Water is much closer to permanent water than the other pools surveyed (Table 1), and thus *B. punctatus* dispersing from a more predictable habitat migh be able to reach Coyote Water. They are not typically found very far from predictable water sources (Degenhardt et al. 1996), and may not be capable of travelling far enough to colonize pools farther from permanent water.

Cluster analysis (McCune and Mefford 1999, McGarigal et al. 2000) resulted in four clusters of communities at a dissimilarity distance of 1.3 (Figure 3). Two pools, NN2a, and NI1s, were identified as quite different from all other pools; NN2a contained only spadefoot toad tadpoles, *Spea multiplicatus*, in August, and NI1s contained only Chironomidae larvae in September. The two borrow pits were clustered, but widely separate from the rest of the surveys. These two pools were the only pools containing the water boatman *Callicorixa* sp. in September, and both had simple communities (e.g., 1 species and three species). *Callicorixa* sp. was found in CWa and NI1a, but these pools had diverse communities (10 species and 8 species, respectively), thus *Callicorixa* sp. played a small role in the cluster analysis. Two pools with simple communities sharing the mosquito larvae of *Psorophora* sp. were also identified as fairly similar; NN1a contained only *Psorophora* sp., and DM1s contained this mosquito and larvae of the beetle *Dibolocelus* sp.

The other two community clusters involved more pools, and mostly more diverse communities. Three pools, NN1a, NI1a, and DM1a, all shared Chironomidae larvae, and *S. multiplicatus*. These three pools were first linked to NN2a, based on sharing *S. multiplicatus*, and then linked at a distance of about 1.8, with NI1s which contained only Chironomidae larvae. The other major cluster included the two surveys of Coyote Water, DM2s, and ATs (Figure 3). These were the four most diverse communities, characterized by the fairy shrimps, *Streptocephalus dorothae* and *Thamnocephalus platyurus*. The two Coyote Water communities were more similar to each other than any other pairwise comparison among the 13 surveys, and were linked in the cluster analysis at a distance of only 0.08. The other two pools in this cluster, ATs and DM2s, were also very similar, linked at a distance of only about 0.2. These two pools were the only two with both the tadpole shrimp, *Triops newberryi*, and the mosquito larvae of *Psorophora* sp. (Table 2).

Community analysis of species composition and physical characterisitics of the pools using NMS (Figure 4a and 4b), revealed patterns similar to cluster analysis. The first two axes explained 43.1% of the variability among communities, adding a third axis accounted for 78.1% of the variability in the data. The two borrow pits were grouped together on the first two axes (Figure 4a), but separated by the third axis (Figure 4b); they were distant from all the other communities in ordination space. Diverse communities (six or more species), were located to the left of the center of the two-dimensional space, those pools containing T. newberryi were in the lower left quadrat, those without T. newberryi were in the upper left quadrat. Despite the differences in size (Table 1) these five communities remained fairly close together in three-dimensional NMS space (Figure 4b), primarily because they shared a number of species (Table 2). DM1s, which only had two species, was located very close to DM1a with only the first two axes, but the third axis separated these two communitied completely (Figure 4b). Simple communities were scattered across the plot, depending on presence/absence of spadefoot toad tadpoles (*Spea multiplicatus*), mosquito larvae (*Psorophora* sp.), or Chironomidae larvae (Figure 4, Table 2).

Pool characterisitics that influenced arrangement of pool surveys in NMS included distance to permanent water ($r^2 = 0.392$), current area ($r^2 = 0.263$) and current area-to-depth ratio ($r^2 = 0.249$) on Axis 1; maximum surface area to volume ratio ($r^2 = 0.491$) and maximum depth ($r^2 = 0.316$) on Axis 2; and current depth ($r^2 = 0.117$) on Axis 3. None of these factors were particularly strong. Community locations appear to be structured more by species composition than physical similarities of the pools. The relatively high importance of distance to water compared to most pool size parameters indicates that community composition may be influenced more by colonization events (insect dispersal flights, wind dispersal of cysts, etc.) than predictable parameters such as pool size.

Three factors appeared to be important in determining which species will show up in an ephemeral pool community. Pools in small washes that are frequently scoured by runoff had very simple communities, consisting of species that escape the pool environment and re-colonize following re-filling. Pool size, which may be manifested in analyses as volume, surface area, depth, or area to depth or volume ratios, is representative of how long a pool can hold water, and is correlated with which species can complete their life cycle before a pool dries. Distance from permanent water represents the likelihood of colonization, especially by aquatic insects. Age did not show up in the analyses as an important factor, yet there were some species, notably those with passive dispersal, that were found only in the older, natural pools.

Three pools contained water in both August and September surveys. Deadman Wash 1 (DM1) and the Navajo impoundment (NI) both had very depauperate communities in September (Table 2). The September surveys in these two pools revealed very different communities from those found in August. Sorensen's similarity indices between August and September were 0 for DM1, which shared no species between the two surveys, and 0.111 for NI, which shared one species between the two surveys. Coyote Water (CW) was the third pool containing water during both August and September surveys. This pool had the most diverse aquatic community of any pool, with 10 species in August and nine species in September (Table 2). Six species were present during both surveys (Table 2) and the similarity between the two communities was much higher than the other comparisons ($S = 0.632$).

Prior to the first surveys, 27.2 mm of rain fell between 3 and 14 August 1997 at the Wupatki NM Visitor Center (Anonymous 1997). DM1a was surveyed on 15 August, the other five pools were surveyed on 16 August 1997. Maximum water depth of DM1a on the 15th was 3 cm, and volume was estimated to be approximately 126 l of water with a surface area of about 4.2 m^2. By the evening of 16 August, this pool had shrunk to about 5 l, and was probably completely dry by the evening of the 17th. The Navajo Impoundment was estimated to contain about 467 l on 16 August, with a maximum depth of 20 cm and a surface area of about 2.3 m^2. This pool was also probably dry within a week of being surveyed in August, since only 6.6 mm of rain fell at the Visitor Center in the week following the August survey, and daily high temperatures were above 32*C for the week (Anonymous 1997).

Coyote Water had an estimated surface area of 33.8 m^2, with a maximum depth of about 54 cm, and an estimated volume of 10,740 l. Given the volume of water in Coyote Water, it is unlikely that this pool dried completely before the September survey. On 18 August, 6.6 mm of rain were measured at the visitor center; no rain fell for a week after that (Anonymous 1997). Between 25 August and the 17 September surveys, 62.5 mm of rain fell, which probably kept Coyote Water from drying up before the September survey.

If DM1 and NI dried completely between filling rain events, their aquatic communities would have to be re-assembled entirely. This probably accounts for the lack of similarity between August and September communities in these pools. Both pools had branchiopod crustaceans present in August (Table 2), no branchiopods were observed in either pool in September. Presumably there were still cysts of these species in the sediment. All other species found in August would have to disperse out from DM1 and NI as these pools dried, and disperse back to the pools following more rain. It rained 13 times between 17 August and 17 September at the visitor center, a total of 69 mm (Anonymous 1997). Over half of the rain falling in this period fell in the seven days immediately prior to the 17 September survey. The survey probably took place as communities were still forming, some species had not dispersed to the pools yet, some species had only recently hatched and were too small to be caught in the net. It is also possible that the phenology of some species does not involve dispersal in late summer or fall. No spadefoot toads were seen in or near any pool in September, and only one red-spotted toad metamorph remained at Coyote Water in September. The beetles *Berosus* sp., *Hydrochus* sp. and *Rhantus* sp. were present only in August, while *Dibolocelus* sp. and *Hydrophilus* sp. were found only in September. Both *Buenoa* sp. and *Cenocorixa* sp. were likewise found only in September surveys (Table 2).

The simplicity of the communities in DM1 and NI in September may have been due to less time available for dispersal and growth or to the lack of appropriate cues for colonization or hatching. The fact that DM2s, only about 200 m downstream from DM1s contained seven species (three species of branchiopods and 4 species of insects) would indicate that conditions for breaking diapause and stimulating dispersal had been met in the vicinity of DM1. There was much more water in DM2 than in DM1 in September (Table 1).

The difference in quantity of water in DM1 and DM2 during the two surveys also points out the extreme variability in spatial coverage of precipitation events at Wupatki NM. These two pools receive runoff from the entrance road as well as from side cañons and sections of the main cañon. Rain in early August fed DM1, but DM2 was completely dry, while in September, DM1 had very little water and DM2 was a very large pool. The cinder dam separating these two segments of Deadman Wash is slightly upstream of a side cañon flowing from north to south; most of the side channels flow from south to north. The rain that fed DM2 may have fallen mostly north of Deadman Wash, runoff coming into DM2, but little rain fell in the watershed of DM1 during that same period.

If Coyote Water did not dry completely between the August and September surveys, species present in August were not forced to leave, thus communities in August and September were more similar than if all species had been forced to leave between the two surveys. The four species present in August but absent from September communities at Coyote Water included the spadefoot *S. multiplicatus*, the beetles *Hydrochus* sp. and *Berosus* sp., and the water boatman *Callicorixa* sp. (Table 2). Of these four species, only *Callicorixa* sp. was observed in any September survey, being found in the two borrow pits in September. *Spea* and *Berosus* were present as larvae in August. Spadefoot toads develop rapidly, and do not necessarily stay right at a pool after they metamorphose (Ruibal et al. 1969, Dimmitt and Ruibal 1980); it is thus not surprising that they were not observed in September at Coyote Water, or any other pool (Table 2). The *Berosus* sp. larvae may have pupated between August and September surveys, and the adults dispersed, or possibly the pupae were in the sediment and thus unobserved. The *Hydrochus* sp. adults found in Coyote Water in August could have recently dispersed to the pool, but did not lay eggs that would result in larvae being present in September, or they may have already developed in the pool and dispersed out of the pool before the September survey occurred. It is significant that *Hydrochus* sp. was found in three pools in August surveys, but was not found at all in September. The phenology of *Hydrochus* sp.'s life cycle may have kept it from occurring in September surveys, even if a pool doesn't dry out.

In September, nine species were observed in Coyote Water (Table 2), including three species that had not been seen in August. These species were *Dibolocelus* sp. (a beetle), the backswimmer *Buenoa* sp., and the dragonfly *Pantala* sp. Both *Dibolocelus* and *Buenoa* were found as adults, *Pantala* occurred as a nymph. None of these species occurred in any pool in August, and Coyote Water was the only pool where *Buenoa* sp. and *Pantala* sp. were found. These species may require more rainfall before they disperse than other species, and thus had not been induced to disperse from permanent water by the time the August surveys were conducted.

Coyote Water had 13 species in it over the two surveys, far more than any other pool (Table 2). In both August (10 species) and September (9 species) surveys, more species were found in Coyote Water than any other pool surveyed. Five of 22 species were found only in Coyote Water. Coyote Water is fairly old (estimated to be at least 100 years old); species that disperse slowly (e.g., branchiopods, *Bufo punctatus*) have had a longer time to colonize Coyote Water from other water bodies. This impoundment is also near permanent water and relatively large. Species that disperse in response to precipitation (e.g., many insects), and species with low vagility (e.g., *B. punctatus*) would have a shorter distance to travel from refugia, and would be more likely to detect Coyote Water because of its size than smaller pools. These three factors, size, distance from water, and age, probably combine to account for the higher diversity in Coyote Water.

The five species found only in Coyote Water, *Gerris* sp., *Pantala* sp., *Callibaetis* sp., and *Berosus* sp., are typically associated with relatively long-lasting bodies of water, if not permanent water (Usinger 1956, Thorp and Covich 1991, Williams and Feltmate 1992, Anderson et al. 1999). Of 112 rock pools surveyed 1-17 times in the past 12 years, in southeast Utah, *Gerris* sp. occurred only in two pools, *Pantala* sp. in 16 potholes, *Berosus* sp. in 17 potholes, and *Callibaetis* sp. occurred in 23 rock pools (T. B. Graham, Pothole communities on the Colorado Plateau: biological and physical correlates to large branchiopod occurrence, submitted to this volume). The fifth species, *Bufo punctatus*, is often found breeding in ephemeral pools, but typically is not found at very isolated sites ((Degenhardt et al. 1996), T. B. Graham pers. obs.).

Interest in the macroinvertebrate communities of ephemeral pools in Wupatki NM came originally from speculation about whether constructed catch basins were colonized by branchiopods. Because fairy shrimp in particular can build up very large populations, there has been speculation that if constructed catchments contained branchiopods, the indigenous people might have used them as food. While it is not possible to know what invertebrates colonized the catch basins while the Sinagua or Navajo cultures were using these basins, it is likely that at least some insects did immigrate to the catchments when they filled with rainwater. Likewise, it is not known if any of the invertebrates were used as food once they arrived in the pools. Fairy shrimp populations can be very large, and represent a potential source of protein and energy. Recent work has documented that fairy shrimp and brine shrimp were used by other Native American cultures in Idaho and California. This was determined by conducting DNA studies of organic residues found on metates, this could be done on WUPA artefacts as well.

CONCLUSION

Of the predictions listed above, 1, 2, 3, 6 and 8 are backed up by data collected in this study. Number 5 was not confirmed; there were not enough data or pools to address 4 and 7, although the surveys of Coyote Water in August and September support the prediction that additional rains extending the life of a pool may lead to more species using the habitat. Coyote Water had a more diverse community than the Navajo Impoundment, despite their similarities in age (Table 2). Coyote Water is much larger, but perhaps more importantly, it is closer to permanent water than NI is. At least during this study, it also appeared that CW lasts longer.

Ephemeral pool ecosystems are, by definition, transitory and thus organisms inhabiting these systems must re-colonize a particular basin every time it fills with water. Some species, such as branchiopod and ostracod crustaceans, and some insects, occupy the site continuously, entering dormant stages when the pool dries. Other species, e.g., most aquatic insects and amphibians, must disperse from more permanent aquatic refugia, or from terrestrial habitats, when ephemeral pools start to form. Whether dispersal occurs, or dormancy is broken following a particular rain storm depends on whether the event provides the appropriate stimuli to trigger dispersal or to end diapause. Each rain event creates a different environment in an ephemeral pool basin. The maximum size of the pool rarely changes, but actual volume of water that enters and thus the size of the aquatic habitat created, depends on amount of rain that falls each time. How long that aquatic habitat lasts also depends on how much rain falls, as well as the evaporation rate (and thus temperature). Environmental conditions change with every precipitation event, and each combination is probably unique. The composition of an ephemeral pool community is the result of the physical characteristics of the basin, season, and precipitation characteristics, in addition to the composition of the pool of potential colonizers. Some of these factors have predictable influences on pool community structure, e.g., age of basin, physical characters of basin, season of precipitation. However, where it rains on a landscape, how much precipitation falls in an event, and when within a "rainy season" rain actually falls are stochastic factors. Likewise, which species are capable of emigration, and which are physiologically inclined to disperse in response to a precipitation event may vary considerably with time of year, temperature, recent precipitation history, as well as other factors. While there may be some species that will predictably be present or absent during a particular wet cycle depending on the predictable factors, ultimately, the aquatic community in a pool after a particular filling event will be a randomly assembled subset of the pool of potential colonizers.